Bifurcation into Functional Niches in Adaptation

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Abstract One of the central questions in evolutionary biology concerns the dynamics of adaptation and diversification. This issue can be addressed experimentally if replicate populations adapting to identical environments can be investigated in detail. We have studied 501 such replicas using digital organisms adapting to at least two fundamentally different *functional* niches (survival strategies) present in the same environment: one in which fast replication is the way to live, and another where exploitation of the environment's complexity leads to complex organisms with longer life spans and smaller replication rates. While these two modes of survival are closely analogous to those expected to emerge in so-called *r* and *K* selection scenarios respectively, the *bifurcation* of evolutionary histories according to these functional niches occurs in identical environments, under identical selective pressures. We find that the branching occurs early, and leads to drastic phenotypic differences (in fitness, sequence length, and gestation time) that are permanent and irreversible. This study confirms an earlier experimental effort using microorganisms, in that diversification can be understood at least in part in terms of bifurcations on saddle points leading to peak shifts, as in the picture drawn by Sewall Wright.

1 Introduction

While a single habitat can support different niches (different ways for organisms to "make a living" [11]), a single niche can only be occupied by one species [5]. If a species invades a new habitat, what factors influence niche choice? Is this choice reversible? Would the same choice happen if the experiment could be repeated? These are just a few questions that arise when studying the adaptation of populations to novel environments, and they can all be translated into questions about the nature of the fitness landscape that the population invades or inhabits.

Sewall Wright [13–15] developed the idea of a fitness landscape to depict the process of adaptive evolution as that of climbing peaks and passing over saddles to reach higher peaks in the fitness landscape. Though it is a metaphor that tremendously simplifies the topology of genetic space, it is useful as a starting point to think about the dynamics of adaptation. If we envision genetic spaces as vast empty spaces peppered with an exponentially large number of overlapping fitness peaks, we can map the question "What determines how a species selects a niche?" to "How do evolutionary histories end up taking one path over another in genetic space?" Here, we study adaptation to different

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functional niches in the same habitat for digital organisms implemented with the Avida software [9]. When a population "decides" to fill a particular niche, we can think of the mutational event leading in the direction of this particular fitness peak as a *bifurcation* in evolutionary histories. We are going to pay particular attention to the statistics of this bifurcation, study how distinct populations become after bifurcation, and whether a population is likely to backtrack and select another peak. Analyzing the statistics of this bifurcation would be exceedingly difficult if we were to conduct this experiment with biochemical organisms, such as viruses or bacteria. While bifurcation (in the sense of divergence of trajectories) into different functional niches has been observed in such evolutionary experiments [6], even the twelvefold replication of Lenski's long-term evolutionary lines [7] would not afford sufficient statistics to study this issue in detail.

Digital organisms are computer programs that self-replicate, mutate, and adapt by natural selection [10, 1, 12]. The programs compete with each other for CPU time, the resource that allows them to execute their code and self-replicate. The evolution of these organisms is open ended: Rewards are given for completing certain *tasks* (logical and mathematical operations), but no target goal is specified. Evolving tasks can be viewed as one way to make a living in the digital habitat. More details on the task landscape can be found in the Avida User's Guide [9]. Using Avida, identical initial populations in identical environments can be studied with ease. With such an experimental setup, the question of how the initial population evolves in task space can be addressed by running multiple experiments with identical starting conditions, but that evolve differently due to random mutations.

Previously, a related question has been studied using the Tierra digital life platform by Yedid and Bell [16]. They also studied a bifurcation phenomenon, but because Tierrans cannot evolve functional tasks (no such landscape is provided in Tierra), the bifurcation involved a few distinct evolutionary *fixed points*, genetic blueprints that the evolutionary histories ended up on. However, these are genetic rather than functional traits, and therefore do not represent niches in the sense of evolutionary ecology.

The evolution of the tasks that a population is able to complete in (which defines its location in task space) gives information about what sort of functional niche the population is pursuing in order to increase its fitness. This dymanic corresponds to Wright's notion of scaling peaks and traversing saddles, to reach even higher peaks in the fitness landscape. Do these identical initial populations in identical isolated environments evolve into different functional niches, depending on which random mutations occur and when, or do they all approach the same niche, perhaps along different paths in the fitness landscape that are degenerate as far as tasks are concerned? After a finite amount of time (in theory, populations converge to the highest fitness peak in the landscape after an infinite amount of time), we expect the distribution of initially identical populations to inhabit multiple fitness peaks, as observed by a sustained divergence in mean fitness value. Is this divergence in fitness due to different evolutionary paths, corresponding to different choices of task set, or is it simply due to different rates of approach to the same fitness peak?

Although the task space is much more limited in dimension and complexity than a biochemical fitness landscape, it too should foster complicated behavior, such as multiple possible task sets that result in improved fitness (similar to the distinct fitness peaks in the Wright model). The existence of such different realized task sets, as mentioned above, cannot easily be determined solely from the principles of natural selection and mutation. It is quite possible to imagine a system that always evolves towards the same single set of tasks. For example, if certain tasks that are easily acquired (perhaps because many neutral paths in genetic space lead to fitness peaks corresponding to genomes that can perform these tasks) are also rewarded heavily, we can imagine that evolution always converges on the same outcome.

While we cannot make a well-substantiated prediction about the existence of different realized task sets (realized niches) based on theoretical considerations only, the complex nature of the Avida landscape is likely to give rise to multiple, distinct solutions to the problem of increasing fitness in task space. In most situations, for any complex problem there is generally more than one good solution, if not multiple, distinct optimal solutions. The problem of finding an efficient organism for a given environment should not be any different. When multiple tasks are rewarded equally, identical populations can evolve towards different tasks and thus fill different niches, depending on which mutations occur and when.

2 Materials and Methods

2.1 Evolution of Digital Organisms

Experiments were performed with Avida version 1.99, freely available from http://sourceforge.net/projects/avida/. All default values were used, with the following exceptions: The environment configuration file (see [9]) was set to reward all 78 possible logical tasks equally (type = pow, value = 1.0) along with a small reward for ECHO (type = pow, value = 0.2). The random seed was changed for each run, and the time slice method was set to 0, which implies that organisms did not obtain a reward based on genome length. This is an important choice because the standard setting (reward according to the minimum of the genome's executed and copied size) implies *genome size neutrality* in the replication process, that is, there is no advantage or disadvantage to large or small genome size. With the setting chosen here, there is a strong pressure for organisms to *reduce* their size, which they can do by optimizing the replication technique, or jettisoning any genes that are not strictly necessary for replication. On the other hand, this pressure can be overcome by evolving a sufficient number of tasks that the pressure to reduce genome size can be compensated. The mutation rate (probability of error per instruction copied) was 0.0075, the insertion rate per divide was 0.05, and the deletion rate per divide was 0.05. All evolution experiments started with identical populations (seeded with the default replicator of length 100 included with Avida 1.99) and were run for 50,000 updates. An update is an arbitrary unit of time during which each organism in the population is executed for a fixed average number of instructions (set to 30). The default ancestor's gestation time (time to generate one offspring) is 389 executed instructions, which translates to about 13 updates per ancestral generation.

2.2 Statistical Methods

We ran 501 experiments and recorded the realized niche of each population by determining each population's *task set* (the set of tasks it has mastered). A task is deemed acquired if at least 10% of the population can complete that task at the 50,000th update. We can assume that the population is homogeneous (all members of the population execute the same task set, except for mutants), because, as mentioned earlier, the competitive exclusion principle prohibits more than one species from inhabiting the same niche. We also recorded the standard deviation of the percentage of the population performing particular tasks over the last 5,000 updates. If the standard deviation was less than 10% of the final value for all tasks in the set, then the task is said to be stable; otherwise the task is unstable and is not included in the task set. The standard deviation of the task set also provides a method to measure whether or not two task sets are distinct. For this purpose, the difference between the two averages (over 5,000 updates) is obtained and a 92% confidence interval for the true value of the difference of the averages is calculated. If the confidence interval includes zero, then the tasks

are said to have the same average and are thus not distinct. This test is considered only for stable tasks.

3 Results

An analysis of the 501 experimental runs (replicas) showed that the replicas could be divided into two quite distinct groups: those that improved their fitness by completing multiple tasks (the *complex* group) and another that improved fitness by increasing replication rate (the *simple* group). Of the 501 runs, 39.1% (196) were simple populations and 60.9% (305) were complex. All populations were stable for the last 5,000 updates with the exception of three, which we counted as simple. These three were able to complete at least five tasks, but they did not do so consistently. In addition, many populations had insignificant fractions (on the order of 2–7%) of the populations that were able to perform additional tasks, but as they were never picked up by the majority of the population, we did not consider them according to the criterion for task set identification outlined above.

Figure 1 shows the distribution of tasks performed by the simple (white) and complex (hatched) populations. Of the simple populations, 98% could complete none or only a single task (the maximum number of tasks in the simple group was four by definition). Of the complex populations, 76% of the populations completed between 10 and 12 tasks, with a minimum of 8 tasks and a maximum of 72 tasks (see Figure 1). The fact that the complexity of five tasks neatly separates the two peaks in Figure 1 validates its use as a distinguishing marker. The two distributions are distinct with a high degree of confidence.

Even though the simple and complex groups are significantly different, that does not necessarily imply that a bifurcation has taken place. For example, it is theoretically possible that the simple group consists of replicas that simply take longer to climb peaks that the complex group has already reached. We are going to resolve this issue by studying the phenotypic characters of the population, and the distribution of bifurcation times.

As discussed earlier, there are two primary ways to make a living in the digital world: increase replication speed at the expense of sequence length and any computational

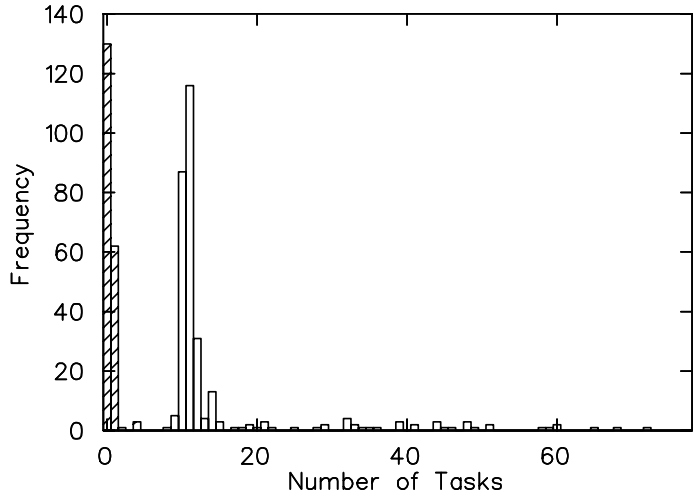

Figure 1. Histogram displaying the distribution of number of different tasks completed by the simple (hatched) and complex (white) populations after 50,000 updates.

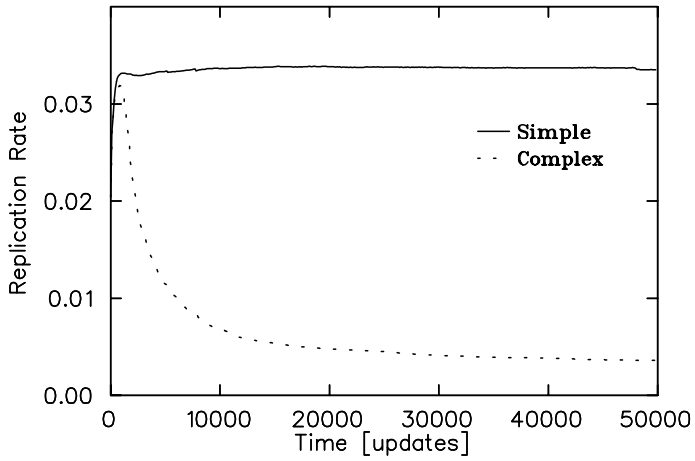

Figure 2. Average replication rate (measured as inverse gestation time) versus time (in updates) for the simple (dashed line) and complex (solid line) populations. The simple population's replication rate significantly increases while the complex population's rate drastically decreases.

genes, or rack up enough computational prowess to overcome the replicatory disadvantage. To test whether the simple and complex groups divide along those lines, we show in Figure 2 the average replication rate for the two groups, as a function of time. It is clear that the two groups' replication rate diverges significantly very early on, and continues to diverge.[1] The two groups also differ significantly in the final fitness achieved (fitness increases exponentially with the number of tasks acquired), and the fitness trajectories also diverge early (see Figure 3).

It is important to observe here that the complex group ends up significantly more fit than the simple group. The minimum fitness achieved by the simple populations was 3.30, with a maximum of 14.89 (mean fitness of 3.79); the minimum fitness achieved by the complex populations was 155.6, with a maximum of 2.53×10^{20} (mean fitness 8.38×10^{17}). This implies that, had the groups been competing in a direct contest, the complex group would always have won. In other words, we must conclude that for the simple group the path towards the complex niche must have been cut off via a *bifurcation mutation* (the putative mutation that led towards the simple peak), because they would surely have been replaced by a complex one had that path remained open.

We can also ask whether the groups differ significantly in sequence length. As we would have surmised from the bifurcation in replication rate, sequence length bifurcates in the same manner, as shown in Figure 4. While the size in the complex group steadily increases as tasks are evolved, the simple group's average size decreases in order to replicate more efficiently. The final size distributions for the two groups (shown in Figure 5) are also significantly different, with a high degree of confidence.

Finally, we can ask about the timing of the bifurcation mutation. If this mutation can occur anytime during the evolutionary history with equal probability, then there is no reason to assume that the simple group cannot either proceed to the complex peak, or "turn back" towards it. In Figure 6, we show a histogram of the time point in the evolutionary history of the complex population when 75% of the organisms were able to complete five or more tasks (the *bifurcation time*). While this bifurcation time

1 Bear in mind that the replication rate displayed in Figure 2 does not translate directly to fitness. While the complex organisms' replication rate (measured as the reciprocal of the gestation time, i.e., the number of instruction executions needed to replicate) decreases, they also acquire enough energy (CPU time) via the performance of computational tasks to speed up this replication sufficiently so that the overall fitness increases.

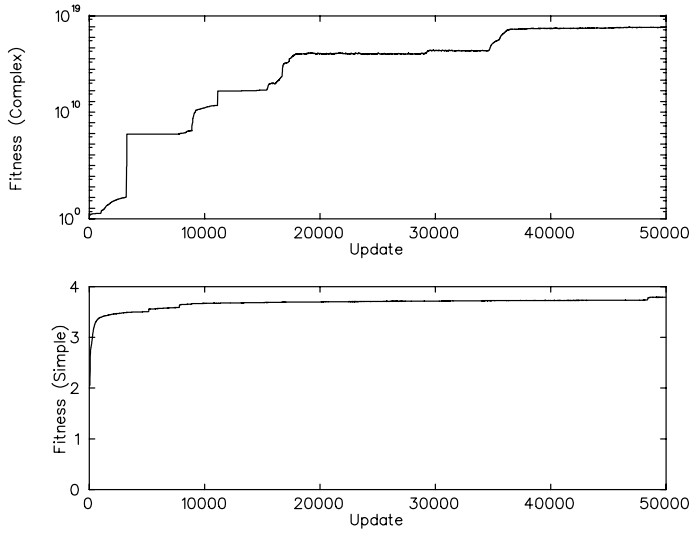

Figure 3. Average fitness as a function of time (measured in updates) for the complex group (upper panel) and the simple group (lower panel).

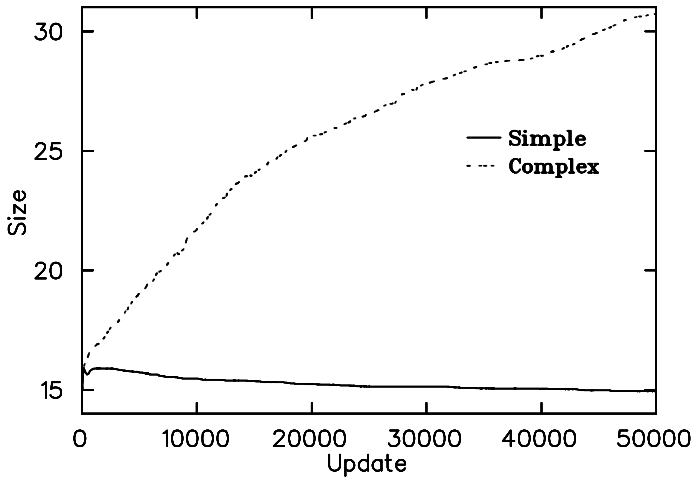

Figure 4. Average size (sequence length) as a function of time (in updates) for the simple (dashed line) and complex (solid) populations.

does not correspond directly to the mutation that actually initiated the bifurcation, we surmise that it is a reasonable proxy that is distributed in a similar manner. Figure 6 shows that most of the runs turn towards the complex niche very early on (92% of the complex populations' bifurcation times lie within the first 20,000 updates). Less than 2% of the complex populations change from simple to complex during the last 20,000 updates. Thus, as the probability of bifurcation decreases exponentially with time, it is reasonable to conclude that the bifurcation is, for all practical purposes, permanent and irreversible.

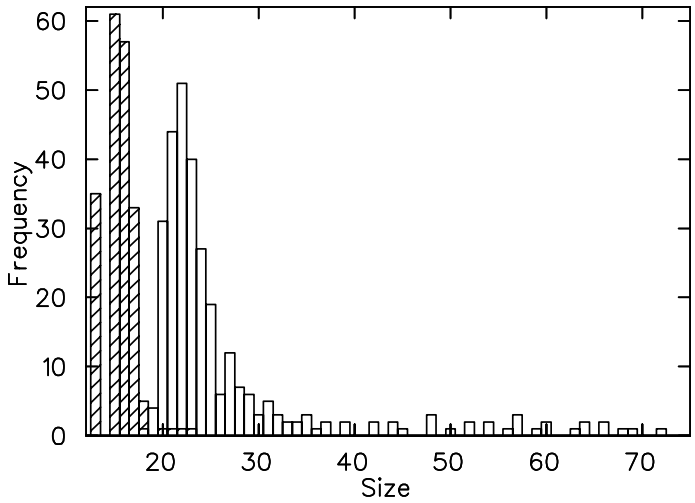

Figure 5. Size distribution for the simple (hatched) and complex (white) populations after 50,000 updates.

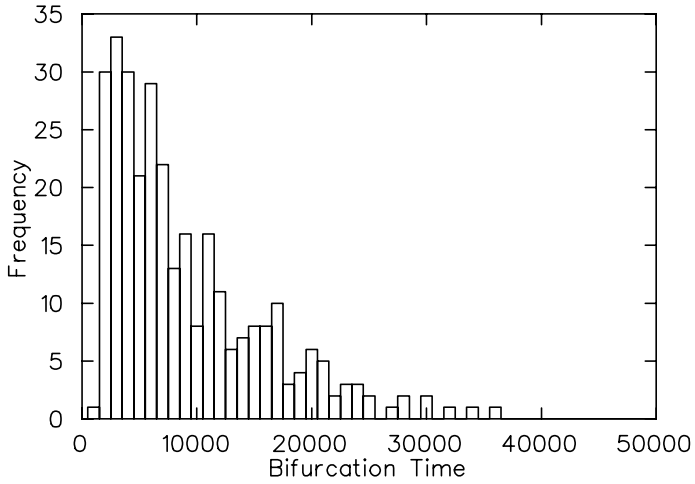

Figure 6. Distribution of the bifurcation time, defined as the update when 75% of the population is able to complete five or more tasks, demonstrating the exponentially decaying probability of a population becoming complex.

4 Discussion

The central question of evolutionary theory concerns the origin of evolutionary changes and diversification. Usually, diversification is thought to be due to adaptation to different environments, random genetic drift, or both. Here, we studied the diversification of initially identical populations that evolve towards very different areas in task space through bifurcations induced by random mutations. This supports the hypothesis that the complex nature of the environment gives rise to different functional niches, that is, different ways to make a living in the same habitat, and that niche selection can be induced randomly. Note that the functional niche concept we use here is different from the standard one, in that two different niches can be occupied at the same time, whereas only one of the functional niches can be occupied.

Although it is clear that the two subsets of simple and complex populations represent two different local peaks in the fitness landscape, this does not rule out the existence

of even more nearby peaks. Indeed, the set of complex organisms most likely occupies different functional niches itself. Although the difference is more subtle than the difference between the two modes exploited by the simple and complex populations, we can imagine the evolution of two different populations (once again from identical initial conditions and in identical but isolated environments) in task space resulting in quite distinct task sets, corresponding to separate task peaks. These distinct functional niches (as defined by the set of tasks they can complete) cannot, however, be distinguished just by the number of different acquired tasks, since the histogram of number of tasks (Figure 1) consists of two peaks corresponding only to the simple and complex populations, with no other immediately apparent feature. The difference between functional complex niches would have to be ascertained by clustering organisms according to patterns of resource use, as is done in [2].

It is likely that there is a critical point in the evolution of the population (the bifurcation point) where a beneficial mutation (or mutations) irreversibly leads towards the complex peak. If this mutation does not occur early, the present study suggests that it will become exponentially unlikely for the population to take this path, as evolution has forced it into an area of genetic space far removed from the path leading to complexity. In other words, it seems that the population starts in what we can deem to be an analogue of a *saddle point* in Wright's fitness landscape that is unstable, and that leads to higher fitness peaks in at least two different directions. For digital organisms, it should be possible in principle to identify, for each population, the crucial mutation that leads to the bifurcation. Such an analysis could conceivably provide insight into microscopic factors affecting the bifurcation.

The simple and complex populations follow survival strategies that are directly analogous to MacArthur and Wilson's r (simple) and K (complex) selection model [8]. Although both populations have the same density, the strategies they each pursue and the characteristics they develop are very close to those described by r and K selection theory: simple population organisms have smaller genome sizes and replicate rapidly while consuming little resource (in the form of computation time), while the complex population consists of organisms with larger genome sizes that replicate slower, consuming more resources. These characteristics can be easily seen in Figures 2 through 5. However, none of the selection pressures usually associated with r or K selection are present in this case. The standard model implies that r selection, for example, is more prevalent in unpredictable environments where resource availability can change drastically, while K selection dominates in stable predictable environments. Density dependent selection is another factor biasing population into either the r or the K mode of existence, with r selection favored in habitats where the carrying capacity has yet to be reached.

In the experiments we have discussed, the two populations faced identical environments, and yet 60% of the populations chose a K type of existence whereas 40% remained in r mode. That r or K type niche selection can depend solely on random bifurcation mutations rather than environmental pressures seems to imply that standard ecological theory should consider stochastic effects along with deterministic causes in the factors affecting reproductive strategies.

We should not go so far as to hypothesize that most of evolution is driven by peak shifts induced by random mutations. Indeed, in the present study we created an environment with a bias towards instability by the choice of time slicing method. Had we chosen the default (length neutral) time slicing, the benefit of sequence reduction (leading to the r lifestyle) would be much reduced, and we would expect a smaller (but non-vanishing) percentage of populations leading the simple life. It would be interesting to test the effect of small changes to the environment on the bifurcation time and percentage in the future.

The present study also corroborates experimental work in evolution that suggests that replicate populations can evolve towards different fitness peaks based on chance effects alone [7]. In the latter study, 12 replicate lines of *E. coli* bacteria were observed for 10,000 generations, and significant and sustained fitness differences between lines were indicative of adaptation to fitness peaks of different height. The present study goes further to imply that the different fitness peaks can correspond to different functional niches in the same habitat. But the conclusions with respect to Fisherian or Wrightian views of evolution are the same. Wright's model [13]–[15] implies a three-part mechanism in adaptation via peak shifts, involving genetic drift. Fisher's [3] and Haldane's [4] view instead focuses on the variation in fitness within a population as a predictor of that population's fitness increase. While we have not carried out a detailed study of this question, it is unlikely that we would find a correlation between genetic variance and the bifurcation into simple and complex in this set of experiments. Instead, the picture that emerges, at least for the type of environment that we created for this study, is one where peak shifts are induced by neutral drift within identical environments: Wright's shifting balance theory.

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